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4. Observations on the Anatomy of a rare Cephalopod (*Gonatus fabricii*). By William E. Hoyle, M.A. (Oxon.), F.R.S.E. (Communicated by Professor G. B. Howes, F.L.S., F.Z.S.)

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(Plates XIII. & XIV.)

Contents.

I. *Introduction.*

The specimens upon which the following investigation is based were as follows :—

1. Three immature examples obtained during the 'Valorous' Expedition, varying in length from 30 to 50 millim.

2. A number of fragments, representing about a dozen individuals, taken by my friend Mr. Robert Gray, of Peterhead, from the stomachs of a Bottle-nosed Whale (*Hyperoodon rostratus*) and a Narwhal. These were for the most part only arms, from which all the hooks and suckers had been removed, with the buccal mass included

between their bases. In two cases parts of the trunk were preserved, but in no instance was there anything like a complete specimen. In consequence, I have been unable to give any account of several organs, and my descriptions of others are lamentably incomplete; but it seemed better on the whole, in view of the rarity of this species, of its unique external characters, and of our almost entire ignorance as to its anatomy, to utilize the material at hand and endeavour to throw light upon the somewhat obscure relationships of this remarkable form.

It is perhaps worth while to mention the order in which the digestive process seems to attack the various parts of the body. The cuticle very soon disappears, then the fin becomes detached, and the posterior end of the pen is dissolved, being probably of a softer consistency than the shaft. Then most of the hooks and suckers become detached, and the tentacular clubs lose the greater part of their armature. The digestive organs and genital glands disappear, and the gills become disorganized, the circulatory organs persisting longer. The head with its attached arms then separates from the body. The nervous tissues are very persistent. The last portions of the body to remain are the mandibles and the lenses of the eyes, which often occur in the stomachs of Cetacea in considerable numbers.

Regarding the external description and history of this Cephalopod I may refer to my 'Challenger' Report[1] and to the authorities therein quoted[2]. The only published information known to me regarding its internal anatomy is about half a page in Verrill's Monograph of the Cephalopods of N.E. America[3]. Its peculiarities are such that I have ventured upon the step of creating a new subfamily for its reception, and it was therefore a matter of special interest to ascertain that this procedure was justified by the internal structure.

For the convenience of the reader I may be allowed to recapitulate here the chief peculiarities of the species, as it will be necessary to refer to them in the subsequent discussion.

1. *The Arms* have each four series of suckers or hooks, whilst all the other Œgopsids have only two.

2. *The Ventral Arms* possess only suckers in all the four series, whilst the other arms have two series of suckers along the margins and two series of hooks up the centre.

3. *The Tentacles* are furnished even from a point low down upon the stem with regularly disposed longitudinal series of small suckers and corresponding fixing-cushions.

4. *The Connective Apparatus* is continued up one side of the club, where it forms a group of five or six large suckers and fixing-cushions, whilst the middle of the club itself is occupied by a very short series of two large and three very small hooks, and the tip of the club is covered with small suckers.

[1] Report on the Cephalopoda. 'Challenger,' Reports, Zool. vol. xvi. part xlvi. p. 174 (1886).

[2] Especially Steenstrup, Oversigt K. D. Vid. Selsk. Forhandl. 1881.

[3] Trans. Connect. Acad. v. p. 393 (1881); also Rep. U. S. Fish Com. for 1879, Washington, p. 418 (1882).

5. *The Gladius* is narrow and linear anteriorly, but broader and lanceolate in the hinder two thirds, whilst it ends posteriorly in a hollow cup or cone, which has several diaphragms within it, and is not covered outside and behind by a solid chitinous spine as is the case with most, perhaps all, Onychoteuthids; at all events no species hitherto known has such a hollow cone.

6. *The Fins* extend some distance beyond the hinder end of the body, and their firm saddle-shaped cartilage slides upon the terminal portion of the gladius.

7. *The Radula* has only five rows of teeth, instead of the usual seven.

II. *General Disposition of the Organs.*

The mantle-cavity is very extensive, reaching backwards almost to the end of the caudal extremity; when it is opened the following arrangement of parts may be observed (Plate XIII. fig. 5). The siphon is of the usual form, having a valve, as has already been recorded by several observers, although Gray denied its existence.

The two retractor muscles of the siphon (*depressores infundibuli*, *m*, *m*) are seen stretching backwards from its base on either side, and external to them are the gills (*br.*), which are very long and fixed to the mantle almost as far as their ends. Attached to the base of the siphon, to the lateral aspect of the head, and to the mantle in the middle line above is the usual valvular flap formed by the collaris muscle, which prevents the egress of the water from the lateral parts of the mantle-cavity.

The ink-sac (*i.s.*) lies in the middle line and extends forwards almost to the anus (*a.*): in the larger specimen it was quite fragmentary, but appeared to reach further backwards than in the small ones, in which, moreover, it was somewhat obliquely placed. The rectum passes over it forwards from right to left, and the anal flaps (in the small examples) are simple in form, and taper gradually from the base to the apex. The vena cava (*v.c.*) lies along the right side of the digestive gland ("liver" of most authors).

Through the renal sac may be seen the sacculations on the vena cava (*re.*) and the branchial hearts (*br.h.*) in their usual situation. The renal openings seem to be minute papillæ, situated just in front of the branchial hearts, as in *Onychoteuthis*. One of my specimens showed them, and I was able with some difficulty to make out their position in a specimen in the British Museum. The apertures of the oviduct (Plate XIII. fig. 3, *od.*) are deeper than and external to the branchial hearts, and the nidamental glands may be seen in the middle line immediately posterior to the renal organs: the posterior aorta passes out between their diverging hind extremities.

In the smaller specimens the stomach (*s*) could be discerned in the middle line behind the bases of the gills; the genital gland when fully developed appears to cover it.

III. *The Cartilages.*

The Cephalic Cartilage.—Two heads of larger specimens were

preserved: in one the cartilage was sacrificed to the dissection of the nervous system, and in the other it had already suffered a good deal of mutilation. I made a sketch of the fragments put together as carefully as possible, and afterwards compared this with the series of sections through the head of one of the smaller specimens. The two figures (Plate XIII. fig. 6) do not therefore represent a drawing of an actual specimen, but have been put together from these two sources.

The basal portion of the cartilage, situated below and behind the united pedal and visceral ganglia, consists of an oblong box with a longitudinal septum down its middle. Each division is produced backwards as a blunt prominence; these are the receptacles in which the auditory organs are lodged. Anteriorly the sides of this box converge and the lower portion of the cartilage comes to consist of a vertical keel, which splits at its lower margin into two plates passing outwards and downwards below the eyeballs. These plates are each perforated near their outer margin by a foramen (*osp.*), which serves to transmit the nerve to the osphradium. At the point where the sloping subocular plate joins the vertical keel is a large foramen (*v.f''.*), which serves for the passage of the veins from the eyes into the large vena cava. Another foramen in the middle line (*v.f'.*) gives passage to the veins from the central nervous system. From either side of the box a vertical plate is given off which lies upon the posterior surface of each eye. The vertical sides of the box are produced upwards and support a horseshoe-shaped plate, the concavity of which is directed backwards. The convexity extends much further forwards than the vertical supporting plates, and arches over a space in which the cerebral ganglia are situated; its anterior extremity is bluntly pointed. There are no basi-brachial cartilages such as are seen in *Sepia*, but there is a thin plate of that material in the dorsal wall of the vena cava behind the cephalic cartilage and quite disconnected from it.

The *nuchal* and *siphono-articular* cartilages (Plate XIII. fig. 7) present no special characters worthy of note. The latter are of the linear kind common to the greater number of Decapoda; they exhibit a tendency to a slight curve, in the form of *f.*

Of more interest is the presence of a pair of cartilages in the ventral wall of the siphon on its outer aspect. These are two thin plates (Plate XIII. fig. 7) of the form roughly of an isosceles obtuse-angled triangle, the median border being straight, the outer expanding to an angle. The sheet of cartilage is thickest near the middle line and thins out gradually towards the side, losing itself in the surrounding tissues. Their formation had not commenced in the smaller specimens: compare Plate XIII. fig. 5.

The *basi-pterygial* cartilages had, however, developed to a considerable extent in these examples. The extremity of the pen lies in a groove between them.

The *pallial* cartilages have a much more intimate connection with the structure of the body-wall than seems to me to have been hitherto recognized. The nuchal cartilage commences as a thin plate which lies upon the muscles in the dorsal median line. Its

upper surface is curved so as to fit into the under surface of the cartilaginous pad which lies below the pen. A little further back (Plate XIV. fig. 1) two processes are seen, one on each side, passing downwards into the muscles, which thus take their origin from them. Still further backwards these processes become longer and pass completely through the body-wall, separating the muscles, which here compose it, into quite distinct masses. The outer limb of the collaris muscle (*co''*.) springs from the notch between the horizontal plate of the cartilage and its vertical process, whilst the inner limb (*co'*.) is attached to the internal surface of the process. As this last lengthens, however, the muscular attachment shifts from the inner surface to the narrow terminal edge of the vertical process.

Three small cartilages which lie below and on either side of the pen will be considered subsequently.

IV. *The Pen.*

The larger specimens presented nothing more than fragments of the stem of the pen, but in the smaller ones transverse sections which were made through the anterior part of the mantle and two series of longitudinal sections through its posterior extremity yielded some information regarding the structure and relations of the pen and pen-sac; and therefore since, so far as I am aware, no observations upon these organs in the Decapoda have hitherto been published, I propose to devote a few words to their description. A transverse section made about a millimetre behind the margin of the mantle is figured on Plate XIV. fig. 1. The pen itself (*p*.) has the figure of an arch with everted limbs, which lies on the whole a little nearer the ventral than the dorsal surface of the mantle. In most instances the process of cutting has produced cracks in it, which indicate its composition of layers parallel to its upper and lower surfaces. It is covered on both sides by an epithelial layer. In the preparations the contraction of the tissues has drawn the lower layer away from the pen, but there can be no reasonable doubt that during life they were in apposition. The upper layer of epithelium (*e'*) consists of very small flattened cells, shortly oval in section and with nuclei of corresponding form; they contain only a small amount of protoplasm. The epithelium below the pen (*e''*), on the other hand, is immensely thicker, consisting of a single layer of elongated columnar cells. The protoplasm of these cells stains more deeply in the distal than in the proximal portion, and is very faintly granular. The nucleus is situated about one third from the proximal end of the cell, and contains a deeply stained nucleolus at its distal end.

The concavity of the arch is partially occupied by a pad of cartilage (*s.nu.*), which is thickest in the middle line and thins away, at first suddenly, then more gradually towards the extremities. The form is such that this cartilage fits exactly into the other one which is embedded in the muscles in the dorsal median line. This is not apparent in the figures because these were drawn from different sections. The two concavities which are due to the eversion of the limbs of the arch are also filled by pads of cartilage (*su.g.*) similar

in histological structure to that just mentioned. The matrix of this cartilage is perfectly hyaline and does not take up the staining-fluid (borax carmine), and there is comparatively speaking a considerable thickness of it between the adjacent cells. In the centre of the cartilage the cavities are subspherical, but towards the surfaces, particularly towards that one which is directed to the pen, they show a tendency to become flattened. The cell-contents appear pale and structureless, and are slightly retracted from the margin of the cavities in which they lie. The nucleus is variable in form and is always pushed quite to one side of the cell, usually towards that side which is directed to the pen. In the two lateral pads of cartilage it is larger, rounder, and more frequently shows traces of cell-division. The inferior surface of the median cartilage is, of course, covered by the epithelial lining of the mantle (*e.m.*), which here becomes ventral and has very distinct round nuclei.

The structure of the pen-sac undergoes various modifications in its different parts. At the anterior extremity (fig. 4), for example, its structure is much simplified. Merely the two layers of epithelium are to be found, but even here the lower one is much thicker than the upper owing to the different form of the cells. At this point no trace of the cartilaginous pads is visible. This preponderating thickness of the lower epithelium may also be observed in embryos, as is shown in several of Bobretzky's [1] beautiful figures. There can be little doubt that it indicates that this lower layer is the one which is active in secreting the pen.

A little further back than the region first described the pen undergoes a slight change in the form of its transverse section. It not only becomes thicker, but each limb of the arch gives off a prominence near its end, towards the middle line, the limb itself being prolonged outwards to a thin sharp edge. Opposite the prominence the lower epithelium is thinner than elsewhere, but it thickens out into a triangular pad between the prominence and the extremity of the limb of the arch, thus forming a kind of mould upon which the pen is shaped.

Still further back, on a level with the stellate ganglia, both layers of epithelium have the same appearance, the inferior one having become reduced to a layer of simple pavement epithelium. This point is posterior to the region of the nuchal cartilages, hence no cartilage is to be seen below the pen. The two upper cartilages have also disappeared, and the concavity of the arch is filled with connective tissue.

The posterior extremity of the pen-sac showed some points worthy of being recorded. This part of the animal was entirely digested away in the larger examples, and the observations here recorded were based upon sections of two of the smaller specimens.

At the posterior extremity of the body both the superior and inferior tracts of epithelium are extended laterally and their edges

[1] Bobretzky, "Izsliedovaniya o Razvitie Golovonogikh" [Investigations on the Development of the Cephalopoda], Izvest. Mosk. Univ. xxiv. figs. 34, 58, 62, 85, 87 (1877).

unite so that each forms a cone, the inferior layer being internal to the superior (Plate XIV. figs. 2, 3). They are not in contact, but a narrow space is left between them, which of necessity has the form of a funnel. Furthermore the internal epithelial cone is truncated, so that a conical space is left between it and the outer cone. In the preparations the epithelial surfaces had shrunk away at many points from the chitinoid material below.

The epithelium lining the pen-sac (e', e'') is, in this region, thin and composed of cubical cells, except at a point near the tip of the pen on the dorsal aspect, where the cells are almost columnar. The appearance of the shell itself does not differ from that seen in the more anterior regions except that it is paler in colour and seemingly softer in consistency, for it does not crack under the razor. A very curious tissue, however, fills up the small conical space, which was described as existing at the extreme tip of the pen-sac (*c.p.*). Immediately lining the epithelium is a layer of normal pen-substance, that is to say, not differing from that seen in the adjacent parts. Within it is the mass of tissue just mentioned (*c.p.*). It consists of a matrix which takes up borax carmine very faintly, but still just sufficiently to mark it off clearly from the chitinoid pen-substance. It presents a series of striations, which pass over it irregularly in very various directions, sometimes straight, sometimes curved. Quite at the posterior extremity an appearance is presented as though the dorsal limb of the pen had been bent sharply backwards upon itself (fig. 3). The matrix contains a large number of vacuoles, of spherical or ovoid form, their long axes, in the latter case, lying parallel with the striations above mentioned. They vary considerably in size. Within the matrix, moreover, numerous nuclei are embedded; but in only one or two instances was I able to make out any cell-substance connected with them, and in these it had a loose granular appearance. Two or three examples showed the cell-substance passing off from the nucleus in the form of radiating threads, such as have been frequently figured in representations of the cartilage of the Cephalopoda; I was, however, unable in the preparations examined to trace the processes of the cells into the matrix. Many of the nuclei could be easily seen to be lying in the vacuoles in the matrix, but many looked precisely as though they were closely surrounded by the matrix itself. This was probably erroneous, for with the highest powers which the preparations would bear the number of cells which could be distinctly seen to be surrounded by vacuities was greatly increased. The conclusion seems to be that we have here to deal with a form of cartilage, but of a degenerate type. It will be interesting to assertain whether any material of similar nature occurs in corresponding situations in *Ommastrephes* and *Onychoteuthis*.

In the other specimen of which longitudinal sections were made (fig. 2) the appearance presented was somewhat different. The matrix had entirely lost its subhyaline as well as its striated look and was evenly granular throughout. Only a vacuole could be seen here and there, and the nuclei also had almost disappeared; so that one might suppose that here the degeneration of the cartilage had

reached a more advanced stage. Another observation, too, indicates beyond a doubt that the process of pen-formation has proceeded further in this specimen than in the other. At the base of this cone the epithelium has been retracted away from it, and on the surface thus liberated could be seen a film of highly refractive material (*sep.*). A similar film is also discernible on the ventral aspect of the base of this cone, and they both become thinner and disappear as they pass towards the centre of the base. I think it is safe to conclude that we have here the incipient formation of the phragmocone which is known to be present at the posterior extremity of the pen of *Gonatus*. The conical mass of degenerate cartilage then serves the purpose of a mould upon which the septa of the phragmocone are deposited.

Near the middle of the granular mass was a curved band of apparently denser material than the rest, in the centre of which a faint line could be traced. Whether this is merely accidental or whether it indicates the position of an earlier incomplete septum I have no means of ascertaining.

V. *The Muscles.*

Regarding the disposition of the muscles not very much is to be said; on the whole it resembles the arrangement found in *Onychoteuthis* and *Enoploteuthis*, but differs from both these in certain respects.

The capsule of the liver, formed by the retractor muscles of the head, is much less strongly developed than in *Onychoteuthis*, the lateral portions being, to all appearance, merely membranous without any muscular fibres. The *retractores capitis mediani* arise separately in their usual situation near the middle line; as they pass forward they approach each other and fuse together a short distance behind the point at which the cephalic aorta enters them; in front of this they are again easily separable. In a specimen of *Onychoteuthis banksii* which was examined for the sake of comparison there is a union in the same place, but less complete.

The *retractores capitis laterales* are slightly developed and they seem to be distinctly separated from the median retractors by a membranous interval in the capsule of the liver.

No muscle is present running from the head to the ventral surface of the pen-sac, and passing over the commissure between the two ganglia stellata, such as is described by Brock[1] in the case of *Enoploteuthis*.

The *collaris* muscle has the usual disposition and relations.

The *adductor infundibuli inferior* has pretty much the same arrangement as in *Onychoteuthis*. It arises far forwards and some distance from the ventral line, and is inserted nearly in the middle line a little distance behind the posterior infundibular nerve.

VI. *The Nervous System and Sense-Organs.*

The *central nervous system* (Plate XIII. figs. 1, 2) resembles most

[1] Brock, "Versuch einer Phylogenie der dibranchiaten Cephalopoden," Morph. Jahrb. vi. p. 198 (1880).

nearly that of *Ommastrephes*, of all those which have hitherto been described in detail[1]. The brachial ganglion (*br.g.*), however, is not quite so widely separated from the pedo-visceral (*p.v.*) as in that genus.

The fusion between the pedal and visceral ganglia is very complete. Buccal ganglia (*b.g.*) are situated upon the posterior extremity of the buccal mass, and are connected as usual both with the cerebral and brachial ganglia. Furthermore there is present a cerebro-brachial connective.

The *Peripheral nerves* could scarcely be made out at all owing to the disintegrated condition of the specimens, but it was easy to see that the brachial commissure is simple as in all Decapoda.

The *Stellate ganglia* are large flattened pyriform bodies; they are connected by a strong and easily recognized commissure. The pallial nerve (*p.n.*) divides a little distance before reaching the ganglion, the main trunk passing directly backwards and reuniting with the nerve given off from the posterior extremity of the ganglion. This arrangement resembles in its general features that figured by Brock[2] for *Ommastrephes* and *Todarodes*, but with certain minute differences.

A number of sections were made of the *Eye*, but they did not exhibit any features calling for special notice.

The *Osphradium* consists of a small antero-posteriorly directed ridge, which is placed below and a little behind each eye; it could be very clearly followed through a number of sections extending perhaps over half a millimetre of the animal's length. The preparations did not show any of the histological features characteristic of the osphradium, but I feel justified in regarding this ridge as such partly because of its position, and partly because just internal to each of these ridges there was a foramen in the cephalic cartilage through which passed a nerve.

The *Auditory Organs* occupy their usual position.

VII. *Digestive Organs.*

The *Beak* is remarkable chiefly for the long curved apex of the superior mandible. It has been figured by Steenstrup, but unfortunately the plate containing it has not yet been published.

The *Radula* has been admirably figured by Sars[3]. It is remarkable as being the only known Cephalopod radula in which only five rows of teeth are present. On comparing it with the radulæ of *Onychoteuthis*[4] and *Enoploteuthis*[5] it appears that the teeth which have disappeared are those situated close to the median tooth ("Zwischenplatten" of Troschel). The median teeth themselves have a long median denticle, and on either side a short acute denticle, so that they resemble those of *Onychoteuthis* rather than of

[1] Compare Pelseneer, "Valeur morphol. des bras, &c. . . . des Céph.," Arch. de Biol. viii. fig. A.

[2] Brock, *op. cit.* p. 226, pl. xi. fig. 7.

[3] 'Mollusca regionis arcticæ Norvegiæ,' pl. xvii. fig. 2 (1878).

[4] Troschel, "Mundtheile d. Ceph.," Arch. f. Naturg. xix. i. p. 11, pl. i. fig. 6.

[5] Brock, *op. cit.* pl. xii. fig. 10 *C*.

Enoploteuthis. The medio-lateral teeth are shorter and less acute than in either of these forms.

The *Anterior Salivary Glands* are present and lie in the form of two ramified glands packed away in the floor of the mouth. Their openings are situated one on either side of the median elevation which forms the floor of the mouth anterior to the radula.

The *Posterior Salivary Glands* are in contact with the inferior surface of the œsophagus, and slightly overlap the cephalic cartilage; they form a pyriform mass, the pointed extremity being directed backwards. The entrance of the duct into the œsophagus was not made out.

The *Œsophagus* (Plate XIII. fig. 4, *œ*) is very slightly fusiform just behind the central nervous system; but it cannot be said that a crop is formed unless the expansion were very much greater than in the examples examined. Another fusiform portion is seen just before it opens into the stomach.

The *Stomach* (*s*) is simple and saccular, more elongated in the larger specimen than in the smaller. In one of the examples from the Narwhal's stomach there was a chitinous lining, which had become completely detached. It appeared to have formed a coating over the whole inner surface of the organ, and is much thinner at the posterior extremity than it is a little way behind the œsophageal opening. There were, however, no dentiform prominences such as I hope to describe elsewhere in an account of the genus *Taonius*. In the same instance it contained a quantity of fragments of Crustaceans, but not one of them was large enough to give any chance of specific determination.

The *Rectum* (*r*) as usual leaves the stomach close to where the œsophagus enters it, and about the same point is the opening of the cæcum. It presents no noteworthy features.

The *Cæcum* (*c*) lies upon the anterior part of the ventral aspect of the stomach, somewhat towards the right. It is coiled into a complete spiral and presents a striated appearance which seems to be due to a series of folds in its lining mucous membrane.

The *Digestive Gland* (*d.g.*, "liver" of various authors) is large and ovoid and has the usual relations. The structure usually known as "pancreas" (*pan.*) is situated in the angle between it and the cæcum and œsophagus.

VIII. *Circulatory Organs.*

The *Heart* (Plate XIII. fig. 3, *v*) is broadly pyriform in shape, the anterior end being somewhat narrower than the posterior; it is directed as usual almost antero-posteriorly, the anterior end being turned a little towards the right. At two opposite points in its largest diameter the heart receives the branchial veins (*br.v*), which as usual pass along the anterior or free side of those organs. There are only two aortic apertures to the heart, which are situated at its anterior and posterior extremities (*a.ao*, *p.ao*); the former gives off the cephalic aorta, quite in the ordinary manner. As regards the vessel from

the posterior end I regret my inability to give a satisfactory account of its distribution, and the more so since it would have been interesting to ascertain how far it agrees with what Brock [1] has indicated as the typical arrangement among the Œgopsida. All that I am able to assert is that this vessel does not branch until a distance of about 2 centim. from the heart; at which point it bifurcates. It seems probable that these two branches represent the anterior and posterior aortæ of Brock, in which case I have failed to discover the arteria genitalis; this, however, is not much to be wondered at considering the state of preservation of the specimens. There were no aortic hearts to be seen in any of these vessels.

The *Vena Cava* (*v.c.*) bifurcates on a level with the anterior part of the ventricle; a branch passing to each branchial heart, at the entrance to which it is joined by a vein passing from behind forwards over the dorsal surface of the branchial heart (*p.v.c.*). A third vein (*o.v.*), beset like the others with renal sacculi, passes over the dorsal surface of the left branchial heart and then turns downwards over the root of the left gill to join the other vessels entering the left branchial heart; it probably comes from the ovary, but it was impossible to make this out with certainty.

The right *branchial heart* (*br.h.''*) is somewhat smaller and more distinctly quadrate in form than the left (*br.h.'*). Each of them bears upon its dorsal anterior margin a small flattened spheroidal pericardial gland (*p.gl.*).

IX. *Respiratory Organs.*

The *Gills* appear, on the whole, to be constructed on the same type as in *Ommastrephes* [2], as was noticed by Verrill.

X. *Excretory and Generative Organs.*

Regarding the *Renal Organs* nothing more of any importance was made out than has been noted above (p. 119).

But little can be said regarding the generative organs. The two larger specimens which I examined were both females, as was shown by the presence of the *oviducts* (Plate XIII. fig. 3, *od.*). There are two of these, which are gently curved and pass forwards just external to, and on the dorsal surface of, the root of each gill. Their extremities are pointed and the opening is a slit on one side of the tip.

Nidamental glands are present as two flattened sausage-shaped bodies, with their convexities directed towards each other, in the middle line. They present the usual lamellar structure.

Regarding the male organs Verrill makes the following statements:—"The specimen is still immature, and probably only one year old. The spermary or 'testicle' is small (length 18^{mm}, diameters 2^{mm} and 4^{mm}), flattened, tapering backward, partly

[1] *Op. cit.* p. 247.

[2] Joubin, "Struct. et dével. de la Branchie des Céph.," Arch. Zool. exp. (2) iii. 1885.

enclosed by the hooded portion of the pen, and with the anterior end attached laterally to the posterior end of the cæcal lobe of the stomach. The prostate gland, vesiculæ seminales, and spermatophore-sac are small; the efferent duct is long and slender, extending forward over and beyond the base of the left gill."

XI. *The Funnel-Organ.*

This apparatus has been the subject of one or two communications within the last few months, and hence it seemed desirable to make what contributions to the subject were possible from the material at hand. Its history may be dismissed in a few words, since Dr. Brock has recently gone into this matter somewhat fully [1]. It seems to have been first observed by Heinrich Müller [2], who observed it in a large number of species during a sojourn at Messina in 1852. He describes the macroscopic appearance and gives some account of the minute structure. It consists of a median and two lateral pads. "Their surface," he says, "is made up entirely of spindle-shaped corpuscles. . . . . They present great similarity to the nettle-organs of other animals, but are devoid of a filament . . . They are developed in the interior of cells, in which they are often twisted and coiled in various ways." No suggestion regarding their function is here propounded.

Franz Boll [3], in his classic "Vergleichende Histiologie des Molluskentypus," devotes a page to the consideration of the topic. He confirms Müller's account, and points out in addition that the fusiform corpuscles (which he figures) become surrounded by an excretory vesicle ("Secretbläschen"). He compares them with the rod-like bodies found in the epidermis of the *Turbellaria*, but makes no suggestion as to their proper function.

In 1877 Bobretzky [4], in his finely illustrated work on the development of the Cephalopoda, figured sections of the organ in the embryos of *Loligo*, and referred to it as a "thickening of the epidermis (? rudiment of the funnel-organ)."

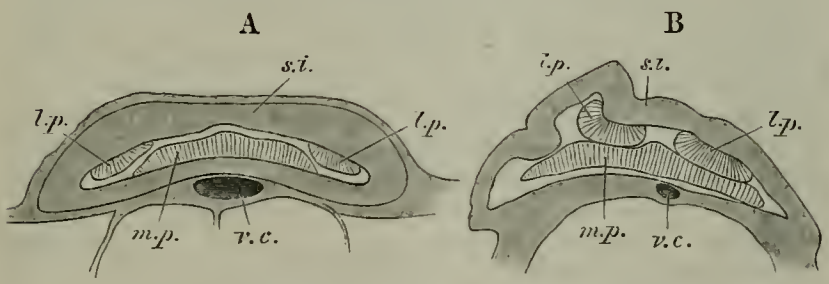
In 1881 Prof. A. E. Verrill [5] described a very highly developed form of this apparatus in the cases of *Taonius pavo* and *T. hyperboreus*. Shortly afterwards I was able to show that a similar structure is present in all the species of that genus [6], and, being at that time ignorant of the previous accounts of it, proposed to give it the name of "Verrill's Organ." In the light of our present knowledge it seems inappropriate to continue the use of this name, and perhaps the proper course to pursue would be to make use of the name funnel-organ ("Trichterorgan"), which occurs in the pages of the earliest writers upon it.

[1] Nachrichten Göttingen, No. 17, 1888, 3 pp.
[2] Zeitschr. f. wiss. Zool. iv. p. 339 (1853).
[3] Arch. mikr. Anat. v. Suppl. p. 97 (1869).
[4] *Op. cit.* figs. 52, 55, 57, 74, and especially 83.
[5] "Cephalopods of N.E. America, II.," Trans. Connect. Acad. v. pp. 413, 432, pl. lv. figs. 2 *d*, 4 *a*.
[6] *Loligopsis* and other genera," Proc. Roy. Phys. Soc. Edinb. viii. 1885.

The only other recent addition to the literature of the subject is a short paper by Malcolm Laurie [1], which adds little of importance to our knowledge.

A large number of the transverse sections which I made through the anterior region of one of the small specimens of *Gonatus* showed the funnel-organ. Its state of histological preservation was far from satisfactory; indeed its extreme sensitiveness to the ordinary reagents has been remarked by all those who have examined it in the fresh condition. Since, however, it is unlikely that any one will have the opportunity in the near future of examining this species in a state of nature, it seems better to place on record the facts observed, so that they may serve at all events for comparison.

This organ is mainly due to a great thickening of the epithelium of three areas in the funnel. One of these is median and lies upon the large venous sinus which passes down the ventral aspect of the animal, separated from it merely by a thin membrane, whilst the other two occupy portions of the two lateral walls of the funnel and are so situated that when the funnel contracts they become applied to the median portion of the organ (compare woodcut).



A. Transverse section through the funnel of an advanced embryo of *Sepia*, to show the form and disposition of the funnel-organ.—B. A similar section of a young specimen of *Taonius*. *m.p.*, median pad; *l.p.*, *l.p.*, lateral pads; *si.*, ventral wall of the funnel; *v.c.*, vena cava.

The cell-boundaries in my sections are very difficult to make out (Plate XIII. fig. 8); they are most distinct in the lateral portions of the median pad, and here it is clear that the pad is only one cell thick, its component elements having become extremely elongated. The nuclei are situated at various points in the cell, generally somewhere in its middle third; they are small and do not stain so deeply as usual. The distal extremities of the cells are occupied by curious highly refracting subglobular bodies. No structure whatever could be made out in these globules, even under a $\frac{1}{12}$-inch oil immersion of Zeiss; they seem perfectly homogeneous and do not take up the stain. Over the surface of the cells is spread a thin layer apparently of secreted material. It stains faintly, is dull and turbid and not strongly refractile; its upper surface is often irregular. It is most distinct a little distance from the margin.

[1] Quart. Journ. Micr. Sci. xxviii. 1888.

Towards the margins of the pads the peculiarities of the epithelium gradually disappear. The cells become shorter, their nuclei more deeply stained, and they pass by insensible degrees into the flattened pavement epithelium which lines the rest of the siphon. At the anterior extremity of the organ it is raised up into a free process, which is completely surrounded by the layer of these highly refractive bodies.

I have also examined sections of this organ in the case of *Taonius* both young and adult, in the embryos of *Ommastrephes*, *Sepia*, and *Loligo*. In its general features the minute structure of the organ is the same in all these instances, but it was only in *Gonatus* that I was able to discover the highly refracting globules described above. What the relation of these may be to the fusiform rods described by Müller and Boll I will not attempt to decide at present, but must leave any further histological discussion till an opportunity offers for describing its structure in *Taonius* and other forms where it is highly evolved.

I shall, however, venture a suggestion as to the function which it possibly discharges, because a hypothesis, even though it may eventually prove to be mistaken, affords a useful guide in subsequent researches. The theories of a sensory or of a phosphorescent purpose in this organ seem to be sufficiently negatived by its situation in a closed space through which only effete products from the body are discharged. Brock is, I think, in error when he states that the main interest of this organ is that it affords an instance of the occurrence in Mollusca of nettle-cells or of bodies allied to them. To my mind the resemblance to nettle-cells is purely superficial. Müller, who noted it, distinctly remarks that they have no filament, and Boll, as above mentioned, did not think that they were so much like nettle-cells as like the rod-bearing cells of the Turbellaria—an opinion which is fully borne out by his figures. The view that the modified epithelium discharges some secretion seems on the whole the most feasible, and is supported by the existence of the structureless layer observed on the surface of the epithelium, which, it may be remarked, is of considerable thickness in the adult *Taonius*. The difficulty hitherto has been to discover the purpose served by this secreted matter.

I would suggest that possibly this funnel-organ is an apparatus for the closure of the funnel, that it is, in fact, functionally, though not morphologically, a valve.

I am led to this conclusion by the following considerations:—

1. The fact that in a very large number of sections which I have examined the pads are so disposed as to very nearly, if not quite, occlude the lumen. I need only refer to the two instances figured in the woodcut as examples.

2. The fact that in those forms in which the organ is most highly differentiated in the adult the valve is absent, as for example in the genus *Taonius*.

3. In this case the presence of a sticky or viscous secretion would be of obvious utility in securing the more perfect apposition of the

surfaces of the pads. This idea is supported by the observations that in some sections the pads could be seen firmly pressed together with a thin line of structureless material between them. The fusiform or rod-like bodies within the cells might be compared with the structures found in those cells of *Cercaria* which secrete the cyst (cellules à batonnet)[1].

The suggestion just made with regard to the function of the funnel-organ is by no means free from difficulties. Of these the most serious is that it persists in the adults of those forms which have a well-developed valve in the siphon. Its discharging one function in the embryo is not necessarily, however, a bar to its having some different use in the adult.

The objection that in those embryos in which it is well formed (*Sepia, Loligo*) there is a valve in the funnel, may be answered by the hypothesis that in these small animals the valve is inadequate. I have seen some sections of *Sepia* in which the valve would certainly be quite insufficient to close the lumen of the funnel, unless this latter were to contract very considerably by its own proper musculature.

Another weighty argument which may be raised is, that this seems a circuitous mode of obtaining the end desired, that if a valve is to be developed it would be best to have it ready for use by the time the embryo quits the egg. Nothing in the way of proof can be urged against this, but it may be remarked that natural processes often seem to us at first sight to be very roundabout in their way of operation. The whole subject is well worthy the attention of any observer who has the opportunity of working it out more thoroughly on fresh material.

XII. *General Conclusions.*

The information now in our hands for instituting a comparison between *Gonatus* and its nearest allies *Onychoteuthis* and *Enoploteuthis* may perhaps be most conveniently summed up in the form of a table. For a number of facts regarding the latter two genera, which I have not had an opportunity of verifying for myself, I must acknowledge my indebtedness to the thesis of my friend Dr. Brock[2].

[1] Sonsino, "Cellules à batonn. de cert. Cercaires," Arch. ital. Biol. vi. pp. 37–61 (1884); Thomas, "Life History of the Liver Fluke," Quart. Journ. Micr. Sci. xxiii. p. 127, pl. iii. fig. 20 (1883).

[2] "Phylogenie d. dibranch. Ceph.," Morph. Jahrb. vi. 1880.

Gonatus.	*Onychoteuthis.*	*Enoploteuthis.*
1. Arms (except the ventral pair) with hooks and suckers (4 rows).	Arms with suckers (2 rows).	Arms with hooks, or hooks and suckers (2 rows).
2. Tentacular club with hooks and suckers.	Tentacular club with hooks and suckers.	Tentacular club with hooks and suckers.
3. Tentacle with connective apparatus along the stem.	Tentacle with connective apparatus confined to base of club.	As in *Onychoteuthis*.
4. The fins extend beyond the end of the body and their cartilage slides upon the gladius.	The fins extend beyond the end of the body proper, but the pointed dorsal process of the gladius extends as far as they do.	The fins do not extend beyond the end of the body.
5. Valve in funnel; also funnel-organ.	Both present.	Both present.
6. Siphono-pallial articulation simple.	simple.	simple.
7. Siphonal cartilage present.	absent.	absent.
8. Pen with phragmocone but no dorsal process.	With phragmocone and dorsal process.	Neither phragmocone nor dorsal process.
9. Musculi retractores capitis mediani fused in middle of their course.	As in *Gonatus*.	Musculi retractores capitis mediani distinct.
10. Retractores mediani distinct from retractores laterales.	Retractores mediani fused with retractores laterales.	Retractores mediani distinct from retractores laterales.
11. Nuchal muscle absent.	absent.	present.
12. Radula with 5 rows of teeth; median like those of *Onychoteuthis*.	7 rows, more complex.	7 rows, less complex.
13. Anterior salivary glands rudimentary.	small.	rudimentary.
14. Anal appendages symmetrical (in young).	asymmetrical.	symmetrical.
15. No accessory hearts on the arteries.	Accessory hearts.	Accessory hearts.
16. Oviducts in number two.	two.	two.
17. Oviducts dorsal to gill-roots.	Oviducts opening into pouch dorsal to gill.	As in *Gonatus*.
18. Nidamental glands present.	present.	absent.

From this table we may extract the following sets of resemblances and differences:—

A. *Gonatus* resembles both *Onychoteuthis* and *Enoploteuthis* in:—
(2) the fact that the club of the tentacle has both hooks and suckers, though it differs widely in their arrangement;
(5) the fact that the funnel has a valve and a funnel-organ;
(6) the simple siphono-pallial articulation;
(16) the number (though not the disposition) of the oviducts.

B. *Gonatus* resembles *Onychoteuthis* and differs from *Enoploteuthis* in:—
(4) the extension of the fins beyond the end of the body proper; though even here a difference in their relation obtains owing to the varying form of the pen, which, however, has a phragmocone in both;
(9) the fusion of the middle portions of the median retractors of the head;
(11) the absence of the nuchal muscle;
(12) the form of the median tooth of the radula;
(18) the presence of nidamental glands.

C. *Gonatus* resembles *Enoploteuthis* and differs from *Onychoteuthis* in:—
(10) the separation between the median and lateral retractors of the head;
(13) the rudimentary anterior salivary glands;
(14) the symmetrical anal appendages;
(17) the situation of the oviducts dorsal to the roots of the gills.

D. *Gonatus* differs from both *Onychoteuthis* and *Enoploteuthis* in:—
(1) the arrangement of suckers in 4 rows and in their armature;
(2) the details of armature of the tentacular club;
(3) the connective apparatus of the tentacles;
(4) the exact relation of the end of the body to the fins;
(7) the presence of a siphonal cartilage;
(8) the form of the pen;
(12) the radula;
(15) the absence of accessory hearts.

In regard to A the most noticeable fact is that no points of importance have been elucidated in which *Gonatus* resembles both the other forms under consideration except such as are also common to a much larger number of forms.

The characters grouped under D are, I think, sufficient to justify the step taken three years ago in making this genus the type of a new subfamily *Gonatidæ*, for there can be no doubt that it is incomparably further removed from *Onychoteuthis* and *Enoploteuthis* than they are from each other.

The question which of these two genera it more nearly resembles is more difficult to settle; but I should be disposed on the whole to attribute more weight to the characters which ally it to *Onychoteu-*

this. The presence of a phragmocone, the absence of the nuchal muscle, the form of the median tooth of the radula, and the presence of nidamental glands are all points of considerable importance, whilst the size of the anterior salivary glands is merely a matter of degree, and the form of the anal appendages in the adult *Gonatus* is unknown. The fusion of the median retractors in one is, so to speak, balanced by their separation from the lateral retractors in the other. The other remaining point, namely the opening of the oviducts into special cavities in *Onychoteuthis*, does not seem sufficient in itself to contravene the resemblances on the other side.

Summary.

In addition to the general sketch of the anatomy of an interesting form, the preceding pages record the existence of several tracts of cartilage hitherto unobserved in the Cephalopoda, and give details regarding the structure of the pen-sac and the development of the pen, as well as new facts regarding the structure of the funnel-organ. The genus *Gonatus* is regarded as being somewhat more nearly related to *Onychoteuthis* than to *Enoploteuthis*, but as much further removed from both than they are from each other. The creation of the subfamily *Gonatidæ* is held to be justified.

In conclusion, I have to fulfil the pleasant duty of thanking Mr. Robert Gray for some of my materials, Professor Huxley for his kindness in allowing me the use of his workroom, and Professor G. B. Howes for the friendly interest he has taken in my work and for numerous acts of kindness during its performance.

EXPLANATION OF THE PLATES.

These letters have the same signification throughout.

a. Anus.
a.ao. Anterior aorta.
br. Gills.
br.a. Branchial artery.
br.h. Branchial heart.
br.h'., *br.h''*. Branchial hearts.
b.g. Buccal ganglia.
br.g. Branchial ganglia.
br.v. Branchial vein.
c. Cæcum.
cc. Cerebral ganglia.
co.', *co''*. Inner and outer limbs of the collaris muscle.
cp. Plug of cartilage in the hinder extremity of the pen-sac.
d.g. Digestive gland.
e', *e''*. Epithelium of the pen-sac.
em. Epithelium of the mantle.
g. Articular groove on the siphon.
i.s. Ink-sac.
m.m. Retractores infundibuli.
nu. Nuchal cartilage.
od. Oviduct.
œ. Œsophagus.
op. Optic ganglia.
op'. Their stem cut short.
osp. Foramen for the nerve to the osphradium.
o.v. Vein probably from the ovary.
p. Pen.
pall.v. Pallial vein.
pan. "Pancreas."
p.ao. Posterior aorta.
p.gl. Pericardial gland.
p.n. Pallial nerve.
p.v. Pedo-visceral ganglia.
p.v.c. Posterior vena cava.
r. Rectum.
re. Renal sacculi on the veins.
ri. Ridge for pallio-siphonal articulation.
s. Stomach.
sep. Rudimentary septum of the phragmocone.
s.g. Stellate ganglia.
s.nu. Supra-nuchal cartilage.
su.g. Supra-gladial cartilages.
v. Ventricle.
v.c. Vena cava.
v.f'., *v.f''*. Venous foramina in the cephalic cartilage.

PLATE XIII.

Fig. 1. The central nervous system and the stellate ganglia, from above: × 2.
2. The same from the side; the stellate and optic ganglia having been removed.
3. The circulatory organs seen from the dorsal surface: nat. size.
4. The digestive tract of one of the small specimens, seen from the side: × 3.
5. One of the small specimens opened down the ventral middle line to show the mantle-cavity; to the right an opening has been made into the renal sac: × 3.
6. The cephalic cartilage; A from the left side, B from above: nat. size.
7. Ventral view of the funnel of one of the larger specimens, to show the cartilages in its wall: nat. size.
8. Part of a transverse section of the median pad of the funnel-organ: × 175; the details added under a higher power.

PLATE XIV.

Fig. 1. Transverse section of the pen-sac and dorsal portion of the body of one of the small specimens: × 175.
2. Somewhat oblique section through the posterior extremity of one of the smaller specimens: the piece of tissue between the pen and the apex of the pen-sac has been included, owing to the obliquity of the section: × 55.
3. Longitudinal section through the posterior extremity of another of the small specimens: × 55.
4. Transverse section through the anterior extremity of the pen-sac: × 175.

March 19, 1889.

Prof. Flower, C.B., LL.D., F.R.S., President, in the Chair.

Mr. W. B. Tegetmeier, F.Z.S., exhibited and made remarks on a specimen of a female Gold Pheasant (*Thaumalea picta*) which had assumed nearly complete male plumage.

Mr. Tegetmeier also exhibited a pair of distorted horns of the Ibex of Cashmere (*Capra sibirica*), in which the horns met in front and crossed each other.

The Secretary laid upon the table a list of the species of Fishes contained in several collections made at Constantinople by Dr. E. D. Dickson, C.M.Z.S., and forwarded to the Society.

The list had been prepared by Mr. G. A. Boulenger, F.Z.S., and contained the names of 66 species; amongst these were two specimens of a species of Trout from Broussa, which, although resembling *Salmo fario*, were, according to Dr. Günther, probably referable to a distinct species. Further specimens, however, were required for their accurate determination.

The Council had agreed to deposit these collections in the British Museum of Natural History in the name of the Society.

The following papers were read :—